

1 **Changing stride frequency alters average joint power and power distributions during**  
2 **ground contact and leg swing in running.**

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13

14 **Abstract**

15 *Purpose.* Runners naturally adopt a stride frequency closely corresponding with the stride  
16 frequency that minimizes energy consumption. While the concept of self-optimization is well  
17 recognized, we lack mechanistic insight in the association between stride frequency and energy  
18 consumption. Altering stride frequency affects lower extremity joint power, however these  
19 alterations are different between joints, possibly with counteracting effects on the energy  
20 consumption during ground contact and swing. Here, we investigated the effects of changing  
21 stride frequency from a joint level perspective.

22 *Methods.* 17 experienced runners performed six running trials at five different stride frequencies  
23 (preferred stride frequency (PSF) twice,  $PSF \pm 8\%$ ,  $PSF \pm 15\%$ ) at 12 km/h. During each trial,  
24 we measured metabolic energy consumption and muscle activation, and collected kinematic  
25 and kinetic data which allowed us to calculate average positive joint power using inverse  
26 dynamics.

27 *Results.* With decreasing stride frequency, average positive ankle and knee power during  
28 ground contact increased ( $p < 0.01$ ) while average positive hip power during leg swing  
29 decreased ( $p < 0.01$ ). Average soleus muscle activation during ground contact also decreased  
30 with increasing stride frequency ( $p < 0.01$ ). In addition, the relative contribution of positive  
31 ankle power to the total positive joint power during ground contact decreased ( $p = 0.01$ ) with  
32 decreasing stride frequency whereas the relative contribution of the hip during the full stride  
33 increased ( $p < 0.01$ ) with increasing stride frequency.

34 *Conclusion.* Our results provide evidence for the hypothesis that the optimal stride frequency  
35 represents a trade-off between minimizing the energy consumption during ground contact,  
36 associated with higher stride frequencies, without excessively increasing the cost of leg swing  
37 or reducing the time available to produce the necessary forces.

38 Keywords: locomotion, self-optimization, step length, joint work

## 39 **Introduction**

40 Runners naturally adopt running kinematics associated with minimal energy consumption,  
41 often referred to as self-optimization (1). Stride frequency is one of the variables naturally  
42 selected and – although highly variable between runners – the preferred stride frequency (PSF)  
43 closely matches the metabolically optimal stride frequency, i.e., the stride frequency that results  
44 in the lowest energy consumption (1–3). Running with a stride frequency lower or higher than  
45 the optimal frequency increases whole-body metabolic energy consumption per distance  
46 travelled resulting in a U-shaped frequency – metabolic cost curve (1–3).

47 While several studies have tried to explain the U-shaped relationship between metabolic energy  
48 consumption and stride frequency, no clear mechanism has been identified yet. Cavagna and  
49 colleagues (1988) (4) found that hopping or fast running animals adopt a stride frequency  
50 slower than the symmetrically bouncing frequency, i.e., the frequency at which the timespan of  
51 the vertical force exceeding body weight equals the time where vertical force is lower than body  
52 weight. While this symmetrical bouncing frequency minimizes the external work (work done  
53 on the body's center of mass, COM), by selecting a lower stride frequency the animals avoid  
54 an increase in internal work (work required to accelerate and decelerate the limbs relative to the  
55 body's COM) associated with higher frequencies. In humans, the optimal stride frequency is  
56 similarly proposed to represent a trade-off between external and internal work as to minimize  
57 the total mechanical work (5). However, this method to calculate total mechanical work based  
58 on the sum of external and internal work largely underestimates the total muscular work (6). A  
59 better approach is to calculate individual joint average powers based on inverse dynamics and  
60 sum all these average joint powers to obtain total lower limb average powers (7,8).

61 While many studies have focused on the energetically expensive ground contact phase, swing  
62 phase cost is likely to be sensitive to stride frequency as well. Running can be divided into a  
63 ground contact and leg swing phase. During ground contact the majority of positive power is  
64 performed around the ankle joint (9) and the leg muscles produce force to support body weight  
65 and propel the body forward (10). While the ground contact phase is energetically the most  
66 expensive phase (11), during leg swing some - mostly hip - muscles are active to swing the leg  
67 forward and consume energy. Several studies have estimated the relative contribution of leg  
68 swing to the net metabolic cost of running ranging from 7 to 26% (11–13). Moreover, Doke et  
69 al. (2005) (14) demonstrated that the cost of swinging an isolated leg sharply increases with  
70 swing frequency ( $\dot{E}_{net} \sim frequency^4$ ) and that positive mechanical work around the hip  
71 strongly correlates with the cube of leg swing frequency ( $R^2 = 0.93$ ). These results suggest that  
72 increasing the stride frequency beyond the optimal frequency may substantially increase the  
73 energy consumption during leg swing and as such increases the overall rate of metabolic energy  
74 consumption. Yet, while this mechanism can explain the increased metabolic cost when  
75 increasing stride frequency above the optimal frequency, it cannot explain the increase in  
76 metabolic cost with decreasing stride frequency below the optimal frequency. Studies  
77 connecting the legs with a spring (i.e. exotendon), finding reductions in energy consumption of  
78 6 to 8 % (15,16), highlight the interaction between joints while running at certain stride  
79 frequency. Simpson et al. (2019) (16) demonstrated that by reducing swing work, through the  
80 exotendon, runners adopt a higher stride frequency reducing joint powers around the ankle and  
81 knee joint during ground contact and leg swing, emphasizing the complex interaction between  
82 lower extremity joints. Hence, investigating the effect of changing stride frequency on lower  
83 limb positive joint power and subdividing these joint powers into ground contact and leg swing  
84 may enhance our understanding on the mechanisms determining the optimal stride frequency.

85 Here we hypothesize that with increasing stride frequency the average positive hip joint power  
86 during leg swing increases while the average positive ankle joint power during ground contact  
87 decreases. In addition, we expect that increasing stride frequency would redistribute positive  
88 joint power from the ankle joint towards the more proximal hip joint. To test this hypothesis,  
89 we used an inverse dynamic approach to calculate individual joint moments and joint powers.  
90 In addition, we measured muscle activity of the ankle plantar flexors as changes in positive  
91 power may reflect in different muscle activations providing more direct evidence of altered  
92 energy consumption.

### 93 **Materials and methods**

94 *Participants.* Seventeen (body mass:  $69.1 \pm 7.7$  kg; height:  $1.79 \pm 0.09$  m; age:  $23.7 \pm 3.8$  y; 13  
95 male; 4 female) injury free subjects gave written informed consent, approved by the local  
96 ethical committee, and participated in this study. All subjects were capable of running 5 km  
97 under 20 minutes ( $16'13 \pm 1'33$  [range: 13'19 – 19'00]) and ran at least 30 km/week.

98 *Experimental setup.* Subjects performed a warm-up on a force measuring treadmill (Motekforce  
99 Link, Amsterdam, The Netherlands) at a self-selected speed for a period of at least 5 minutes.  
100 Next, the treadmill velocity was set at 12 km/h and after several minutes the preferred stride  
101 frequency of each participant was determined by counting the number of strides taken during a  
102 one-minute time interval. This provided the participants with ample treadmill running exposure  
103 before we quantified preferred stride frequency. The average of the three minutes was  
104 considered as the preferred stride frequency. Participants ran six 5-minute trials at a constant  
105 speed of 12 km/h with each trial adopting a different stride frequency (PSF,  $PSF \pm 8\%$  and  $PSF$   
106  $\pm 15\%$ ) enforced by a metronome and verified using the ground reaction force data. Subjects  
107 had 5 minutes of rest between trials. We chose the running speed of 12 km/h based on  
108 Hoogkamer et al. (2016) (17) who had participants of similar fitness running at 3.5 m/s (12.6  
109 km/h) with added mass to their shoes, demonstrated to increase metabolic energy consumption.

110 During the first and last trial, subjects ran at their preferred stride frequency, the stride  
111 frequencies for the four other trials were randomized. During each trial, ground reaction forces,  
112 marker trajectories and whole-body metabolic energy consumption data were collected.

113 *Metabolic energy consumption.* We measured whole-body metabolic energy consumption  
114 using indirect calorimetry (Cosmed K5, Cosmed srl, Rome, Italy). Prior to testing the flow  
115 turbine, oxygen and carbon dioxide analyzers were calibrated according to the manufacturer's  
116 instructions. Rates of oxygen consumption and carbon dioxide production were collected and  
117 averaged over the last 90 seconds. We computed whole-body metabolic energy consumption  
118 (in Watts) using the Brockway equation (18) and normalized energy consumption to subject's  
119 body mass. To allow for reliable calculation of aerobic metabolic energy consumption, subjects  
120 should be running at submaximal intensity which we verified based on the respiratory exchange  
121 ratio. One subject's respiratory exchange ratio exceeded 1.0, indicating that the subject was no  
122 longer running at submaximal intensity, and that subject was discarded for further analysis.  
123 Since the PSF condition was measured during two trials, we took the average whole-body  
124 metabolic energy consumption of both trials, except for one subject where we had issues during  
125 the first measurement and therefore only used the last trial.

126 *Kinetics and kinematics.* Thirteen infrared motion capturing cameras (Vicon, Oxford Metrics,  
127 Oxford, UK) recorded the motion of 48 reflective markers, including four cluster markers on the  
128 thigh and shank, at a sampling frequency of 200 Hz. Ground reaction force (GRF) data,  
129 measured at 1000 Hz, and marker trajectory data were low-pass filtered with a cut-off frequency  
130 of 20 Hz. We used the filtered GRF data to determine ground contact, adopting a 30 N threshold,  
131 and to calculate the actual stride frequency and duty factor (ground contact time divided by  
132 stride time).

133 A marker labeled static trial (Nexus 2.4, Oxford Metrics, UK) was used to scale the Hamner  
134 musculoskeletal model (19) according to the subject's dimensions in OpenSim 3.3 (OpenSim,

135 Stanford, CA, USA). Based on the dynamic marker trajectory data, joint angles were computed  
136 using a Kalman Smoothing algorithm (20). Next, we conducted an inverse dynamic analysis in  
137 OpenSim which, based on the dynamic equations of motion, calculates joint torques. Briefly,  
138 joint torques are computed using the joint angles, ground reaction forces, segment masses,  
139 segment moments of inertia and segment (angular) accelerations. Joint torques were low-pass  
140 filtered using a recursive fourth-order Butterworth filter with a cut-off frequency of 20 Hz and  
141 multiplied by the respective joint angular velocity to compute joint power at the hip, knee and  
142 ankle. After normalizing joint power to the subject's body mass, we calculated positive joint  
143 work by integrating positive joint power with respect to time. To allow for comparison between  
144 conditions, we divided positive joint work during a full stride by stride time to calculate average  
145 positive joint power. Accordingly, average positive joint power during ground contact and  
146 during swing were computed as the positive joint work during ground contact or swing and  
147 divided by stride time. Finally, to calculate the relative contribution of each joint to the total  
148 positive average joint power during the full stride we divided the average joint power of each  
149 joint by the sum of the average positive power of the hip, knee and ankle. Similarly, to compute  
150 the relative contribution of each joint during ground contact, positive average joint power  
151 during ground contact was divided by the sum of positive average joint power of the hip, knee  
152 and ankle during ground contact only.

153 *Electromyography.* We measured the muscle activity of the major ankle plantar flexor muscles  
154 (gastrocnemius medialis, GM; gastrocnemius lateralis, GL; and soleus, SOL) and ankle  
155 dorsiflexor muscle (tibialis anterior, TA) through surface electromyography (Zerowire, CA,  
156 US) with a sampling frequency of 1000 Hz. Before placing the bipolar EMG electrodes  
157 (Ag/AgCl electrodes, 10 mm recording diameter, Ambu), we shaved and cleaned the skin with  
158 alcohol gel. EMG electrodes were placed on the muscle belly of the GM, GL and TA parallel  
159 to the muscle fibers with an inter-electrode distance of 2 cm. The SOL electrodes were placed

160 at 2/3 of the line between lateral condyle of the femur and the lateral malleolus, parallel with  
161 the muscle fibers and 2 cm apart. The raw EMG signal was first band pass filtered (20-400  
162 Hz), rectified and low pass filtered (20 Hz). To compare muscle activation during ground  
163 contact between stride frequency conditions, we calculated the time-integral of the EMG signal  
164 during ground contact. We normalized the integrated EMG signal to the peak amplitude of the  
165 EMG signal, adopting a 10 ms moving average window, of each muscle across all conditions  
166 and for every participant. Finally, to calculate the average activation per unit time during ground  
167 contact, we divided the normalized and integrated EMG signal of each muscle during ground  
168 contact by the stride time. Due to issues with the EMG equipment, we did not record muscle  
169 activation for one participant. We visually inspected all EMG signals for each participant and  
170 for every condition. Five corrupted EMG files were discarded (one participant's GM, one  
171 participant's GL, one participant's TA and two participants' SOL).

172 *Statistics.* All data are presented as mean  $\pm$  standard deviation. Data were first tested for  
173 normality and sphericity using the Shapiro-Wilk test and Mauchly's test, respectively. For  
174 normally distributed data, we conducted a repeated measures ANOVA to test for significant  
175 differences between stride frequency conditions. If the assumption of sphericity was violated,  
176 we performed the Greenhouse-Geisser correction. When the data were not normally distributed,  
177 we executed the non-parametric Friedman test. If a significant main effect was found, we used  
178 the Bonferroni correction for post-hoc testing to identify which conditions were significantly  
179 different from the PSF condition. We also calculated partial eta squared ( $\eta^2$ ) as a measure for  
180 effect size for the repeated measure ANOVA where  $\eta^2 \geq 0.26$  is considered as a large effect. If  
181 repeated measure ANOVA could not be performed due to violations against normality, we  
182 calculated Kendall's W where  $0.3 \leq W < 0.5$  indicates a moderate effect and  $W > 0.5$  a strong  
183 effect. Statistical significance was set at  $p < 0.05$ . An a priori power calculation (G\*Power



184 version 3.1) indicated that, to detect significant changes in average positive ankle or knee joint  
 185 power during ground contact (ES = 0.91 (9) and power = 0.8), we needed 15 participants.

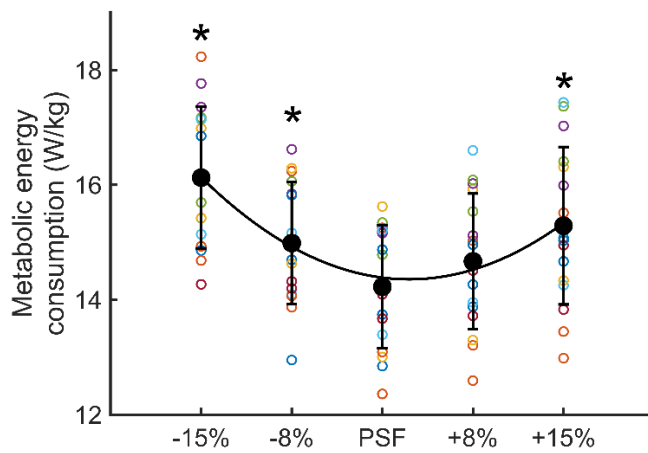
186 *Table 1. Kinematic data as mean  $\pm$  SD for each stride frequency condition (N = 16).*

	<b>-15%</b>	<b>-8%</b>	<b>PSF</b>	<b>+8%</b>	<b>+15%</b>
Stride frequency (strides/min)	73.0 $\pm$ 2.8*	78.2 $\pm$ 3.0*	84.0 $\pm$ 3.2	90.1 $\pm$ 3.5*	95.7 $\pm$ 4.0*
Step length (cm)	137 $\pm$ 5*	128 $\pm$ 5*	119 $\pm$ 5	111 $\pm$ 4*	105 $\pm$ 5*
Ground contact time (ms)	229 $\pm$ 22	227 $\pm$ 18	222 $\pm$ 17	213 $\pm$ 18	206 $\pm$ 17*
Duty factor (%)	27.9 $\pm$ 2.4*	29.5 $\pm$ 2.3*	31.1 $\pm$ 2.3	32.0 $\pm$ 2.6*	32.9 $\pm$ 2.4*

187 \* represents significantly different from the self-preferred stride frequency condition (PSF).

## 188 **Results**

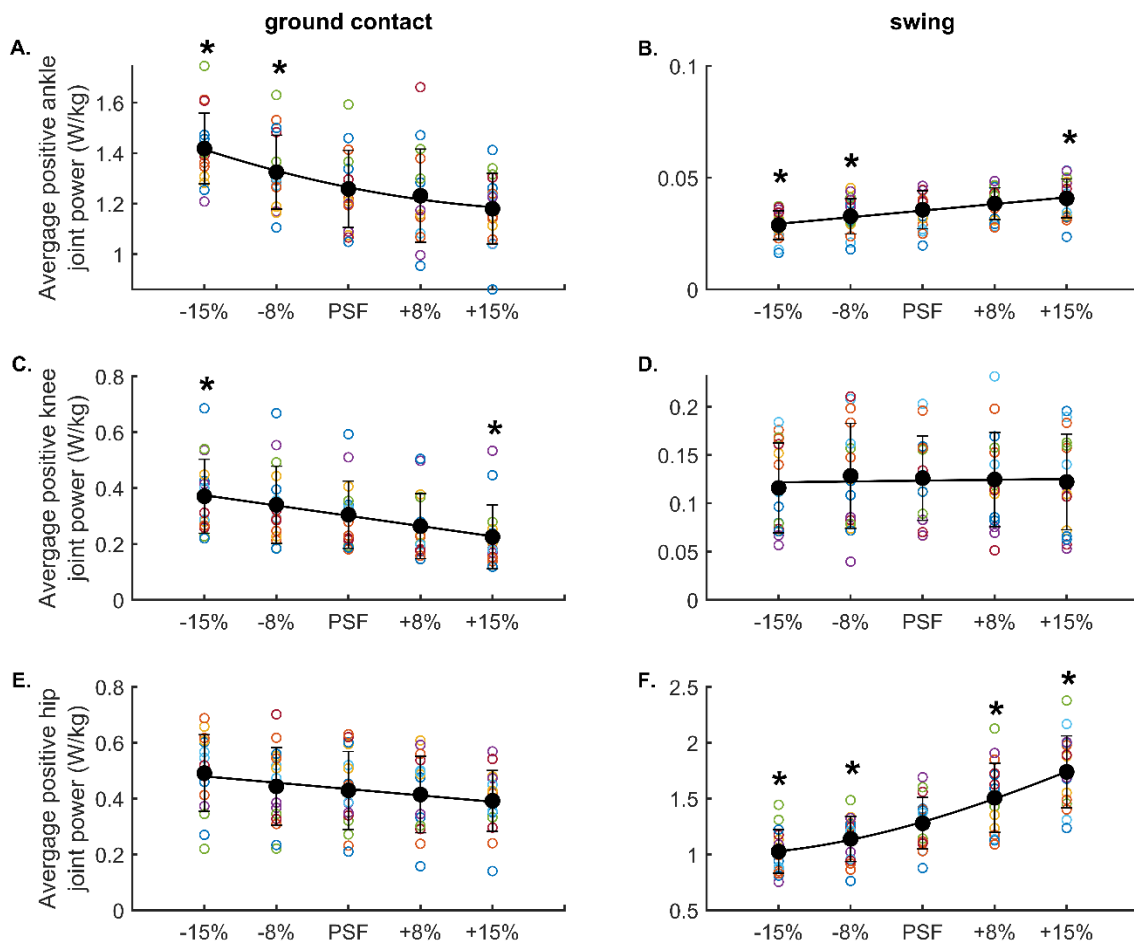
189 Actual stride frequencies were substantially different from the preferred frequency, on average  
 190 stride frequencies were -13.1%, -7.0%, +7.2% and +14.0% different from PSF (Table 1). With  
 191 increasing stride frequency ground contact time significantly decreased ( $p < 0.001$ ;  $W = 0.75$ )  
 192 while duty factor significantly increased ( $p < 0.001$ ;  $\eta^2 = 0.84$ ). Whole-body metabolic energy  
 193 consumption followed a U-shaped curve, with the lowest energy consumption corresponding  
 194 with the preferred frequency ( $p < 0.001$ ;  $\eta^2 = 0.66$ ; Figure 1). Post-hoc analysis revealed that  
 195 energy consumption at all except the +8% stride frequency condition was significantly different  
 196 from PSF. When looking at the individual data, 12 out of the 16 subjects demonstrated the  
 197 lowest energy consumption at PSF. For the other four subjects, three of them showed minimal  
 198 energy consumption when running at PSF +8% and one while running at PSF -8%. Yet, the  
 199 difference in energy consumption between the frequency associated with minimal energy  
 200 consumption and PSF were relatively small for those subjects, within the typical measurement  
 201 error for metabolic energy consumption (21).



202

203 *Figure 1. Metabolic energy consumption across the five stride frequency conditions. Solid black dots represent means and*  
 204 *error bars SD. Open circles are the individual data. \*significantly different from PSF.*

205 Average positive ankle and knee joint power during ground contact decreased with increasing  
 206 stride frequency ( $p < 0.001$ ; ankle:  $\eta^2 = 0.65$ ; knee:  $\eta^2 = 0.75$ ; Figure 2). Post-hoc analysis  
 207 demonstrated that average positive ankle joint power was only significantly different from PSF  
 208 at lower stride frequencies, whereas for the knee joint significant differences in average positive  
 209 joint power were found between PSF and PSF  $\pm$  15%. Running at the lowest stride frequency  
 210 increased average ankle joint positive power by 13% compared to PSF. In line with the increase  
 211 in average positive ankle joint power, the average soleus muscle activation during ground  
 212 contact significantly increased when stride frequency decreased ( $p < 0.01$ ;  $\eta^2 = 0.28$ ; Figure 3).  
 213 Post-hoc analysis revealed that average soleus activation during ground contact when running  
 214 at PSF +15% was significantly lower compared to PSF. We did not find any significant  
 215 difference in average muscle activation during ground contact across stride frequency  
 216 conditions for the other muscles.

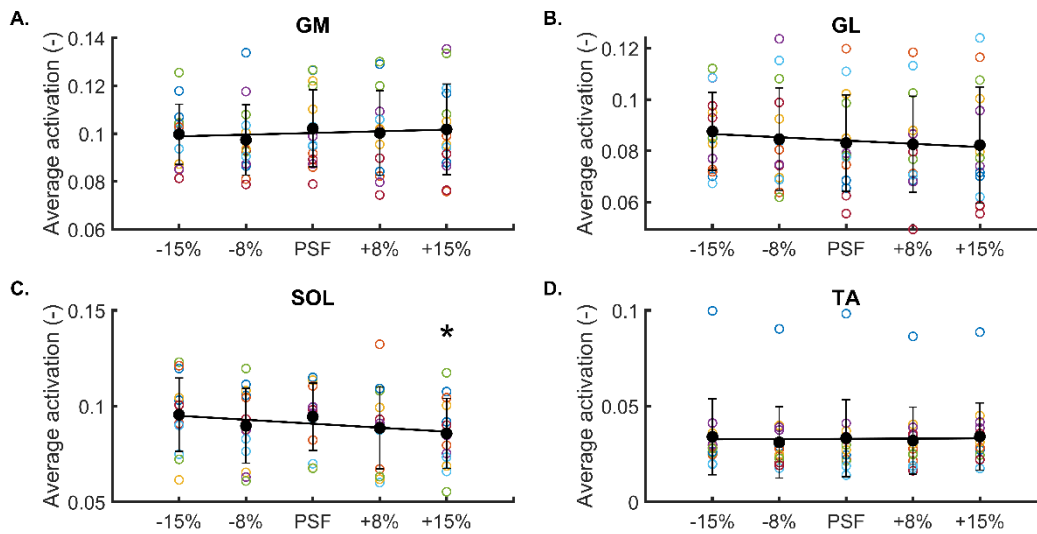


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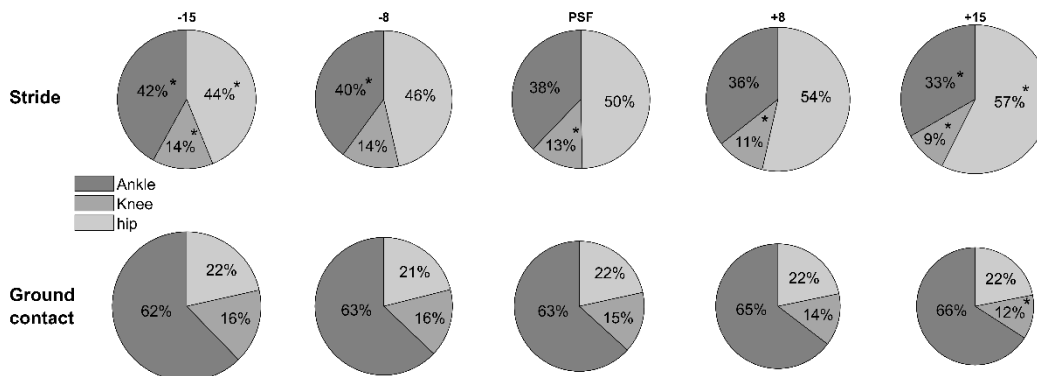
218 Figure 2. Average positive ankle (A,B), knee (C,D) and hip (E,F) power during ground contact (A,C,E) and leg swing (B, D, F)  
 219 during the five stride frequency conditions. Solid black dots are the means and error bars the SD. Open circles represent the  
 220 individual data. \*significantly different from PSF.

221 During leg swing, average positive hip joint power strongly increased with increasing stride  
 222 frequency ( $p < 0.001$ ;  $\eta^2 = 0.81$ ). Post-hoc analysis revealed significant differences in average  
 223 positive hip joint power between all condition and PSF. At the lowest stride frequency, hip  
 224 average positive power was reduced by 20% whereas at the highest stride frequency it increased  
 225 by 36%. As such, the relative contribution of hip average positive power during the full stride  
 226 increased with increasing stride frequency ( $p < 0.001$ ;  $\eta^2 = 0.87$ ; Figure 4), while the  
 227 contribution of ankle and knee reduced ( $p < 0.001$ ; ankle  $\eta^2 = 0.76$ , knee  $\eta^2 = 0.75$ ). In contrast,  
 228 during ground contact the relative contribution of the ankle joint slightly increased with  
 229 increasing stride frequency ( $p = 0.01$ ;  $W = 0.24$ ) whereas the contribution of the knee joint

230 decreased ( $p < 0.001$ ;  $W = 0.53$ ). We found no difference in relative contribution of the hip  
 231 joint during ground contact.



232  
 233 *Figure 3. Average muscle activation during the ground contact phase of running of the gastrocnemius medialis (A.; N = 14),*  
 234 *gastrocnemius lateralis (B.; N = 14), soleus (C.; N = 13) and tibialis anterior (D.; N = 14) across five stride frequency conditions.*  
 235 *Solid black dots are the means and error bars the SD. Open circles represent the individual data. \*significantly different from*  
 236 *PSF.*



237  
 238 *Figure 4. Relative contribution of the ankle (dark grey), knee (grey) and hip (light grey) to the total average positive power*  
 239 *during the full stride (top) and ground contact only (bottom). The radius of each pie chart is scaled based on the total positive*  
 240 *power in each condition. \*significantly different from PSF.*

## 241 Discussion

242 In this study, we investigated the effect of altering stride frequency on average positive joint  
 243 power and positive joint power distribution during the ground contact and swing phase of  
 244 running. We accept our first hypothesis that increasing stride frequency decreases average  
 245 positive ankle power during ground contact but increases average positive hip power during leg

246 swing. With increasing stride frequency, the sharp increase in hip power during leg swing  
247 implied that the majority of positive power during a full stride was provided by the hip. In  
248 contrast, increasing stride frequency also redistributed average positive joint power from the  
249 knee towards the ankle during ground contact. Our results suggest that the mechanisms inducing  
250 the increase in metabolic energy consumption when adopting a stride frequency higher or lower  
251 than the optimal frequency are different.

252 At stride frequencies below the PSF, the large increase in positive ankle power and the small  
253 decrease in positive hip power with decreasing stride frequency might explain why the net result  
254 is an increase in energy consumption. In addition, average positive knee joint power during  
255 ground contact increases with decreasing stride frequency. These results support previous  
256 research demonstrating that decreasing stride frequency increases positive joint work during  
257 ground contact for both the ankle and knee joint (22) and reduces braking forces impulses (23).  
258 The ground contact phase in running is energetically the most expensive phase (11), with the  
259 ankle joint providing most of the positive power during ground contact (Figure 4). Previous  
260 research already estimated that the Triceps Surae muscle, the major plantar flexor muscle,  
261 consumes between 20 and 40% of the total energy during running at the preferred stride  
262 frequency (24,25). Although increases in average positive ankle joint power may be partly  
263 provided by more elastic energy storage and return it will likely increase muscle force or work.  
264 This hypothesis is further supported by an increase in average soleus activation during ground  
265 contact with decreasing stride frequency (Figure 3). Hence, the increase in average positive  
266 ankle joint power, associated with decreasing stride frequency, may increase the energy  
267 consumed by the Triceps Surae during ground contact.

268 Next to the large increase in positive ankle power with decreasing stride frequency, there is also  
269 a relatively large increase in positive knee power which might explain an increase in whole-  
270 body metabolic energy consumption. In absolute terms, the increase in positive ankle joint

271 power with decreasing stride frequency is much larger than the increase in positive knee joint  
272 power, yet there is a change in the relative distribution of joint power during ground contact  
273 (Figure 4). At lower stride frequencies, the relative contribution of the knee increases while the  
274 contribution of the ankle decreases. The Triceps Surae muscle-tendon unit spanning the ankle  
275 joint exhibits a morphology allowing for slow muscle fiber contraction velocities since most of  
276 the length changes in the muscle-tendon unit is taken up by the long, compliant in series  
277 connected elastic element (26–29). In contrast, the more proximal knee and hip muscles lack  
278 those long, compliant series elastic elements and most of the length changes in the muscle-  
279 tendon units are provided by the muscles. Therefore, the hip and knee are suggested to be  
280 metabolically less efficient than the ankle and as such, the increase in positive knee power may  
281 come with a relatively high metabolic cost. While future studies should further look into and  
282 confirm whether different stride frequencies also result in altered muscle dynamics, it adds to  
283 the idea that decreasing stride frequency will make the energy costly ground contact phase even  
284 more expensive.

285 At stride frequencies above the PSF, the small decrease in positive ankle power and the large  
286 increase in positive hip power with increasing stride frequency might explain why the net result  
287 is an increase in energy consumption. Previously, the cost of leg swing has often been neglected.  
288 However, several studies already estimated a substantial metabolic energy cost for swinging  
289 the legs (11–13) and previous research demonstrated that increasing stride frequency leads to  
290 increased maximal hip flexor moment during swing (23). Moreover, adding mass to the leg or  
291 foot alters the inertial properties of the leg and increases metabolic energy consumption during  
292 running (17,30,31). The more distal the mass is added, the greater the increase in energy  
293 consumption (30,31). Doke et al. (2005) (14) revealed that the cost of an isolated leg swing  
294 increases with the fourth power of swing frequency. Based on this, increasing stride frequency  
295 from 84 strides/min to 95.7 strides/min would increase the energy consumption of leg swing by

296 1 W/kg more than the energy consumption decrease by reducing the stride frequency with a  
297 similar amount (from 84 strides/min to 73 strides/min). While the cost of leg swing might be  
298 rather small when running at the preferred stride frequency (i.e. 7-26% of the total metabolic  
299 energy consumption (11–13)), our results indicate that the cost of leg swing may become a more  
300 substantial energetic cost when increasing stride frequency beyond the optimal frequency.

301 Furthermore, our results demonstrate that runners adapt their stride kinetics (i.e. duty factor)  
302 when changing stride frequency, illustrating that the interaction between increasing stride  
303 frequency and metabolic energy consumption is more complex than just average positive hip  
304 joint power. With increasing stride frequency, runners adopt a greater duty factor while running  
305 (Table 1). As such, the relative decrease in ground contact time is smaller than the actual  
306 reduction in stride time, indicating that runners alter their kinetics to prioritize time on the  
307 ground over swing time. Metabolic energy consumption during running is proposed to be  
308 inversely proportional to ground contact time (32,33). Hence, although the positive average  
309 ankle power during ground contact tends to decrease (yet not significantly different from PSF)  
310 when stride frequency increases, energy consumption during ground contact may only slightly  
311 reduce due to the shorter time available on the ground. Similarly, Doke and Kuo (2007) (34)  
312 established that the increase in metabolic cost with increasing leg swing frequency is not only  
313 determined by an increase in mechanical work but also due to a reduction in time to produce  
314 the necessary force, i.e., rate of force development. A greater rate of force development induces  
315 fast muscle activation and deactivation associated with a more energy expensive calcium  
316 pumping (34) and possibly induces the activation of less economical muscle fibers (32,35).  
317 Hence, the shorter time to produce the necessary force to swing the leg forward will increase  
318 the cost of leg swing more than what would have been expected based on average positive hip  
319 power only (34).

320 Some of the limitations of the study are that our participants were trained runners, running at  
321 least 30 km/week on average. Since the PSF of trained runners more closely matches their  
322 optimal stride frequency than the PSF of novice runners (36), not all results may be extrapolated  
323 to novice runners. Next, we calculated average positive joint power and used this positive power  
324 to explain altered metabolic energy consumption. While we normalized the power to time, the  
325 method is still subject to redundancy issues. The inverse approach calculates net joint powers  
326 which slightly underestimates total positive power due to antagonist muscle co-contraction (6).  
327 The muscle redundancy issues also imply that assumptions are made regarding individual  
328 muscle contractile and tendon behavior. Calculated positive power will not always represent  
329 actual muscle power due to passive in series connected elastic tissues performing most of the  
330 work, while muscles primarily produce force (35). Especially around the ankle joint where the  
331 Triceps Surae contracts almost isometrically (29), producing little work, making the muscle-  
332 tendon units around the ankle more efficient for power production (37). Future studies should  
333 use in vivo ultrasound to investigate whether muscle-tendon dynamics change with altered  
334 stride frequencies. Simulation-based studies can estimate individual muscle energy  
335 consumption and provide more insights about how lower leg muscle energy consumption is  
336 altered when running at different stride frequencies. Lastly, we only collected muscle activity  
337 data of the triceps surae muscles because, initially, we were most interested in these muscles.  
338 Yet, our results demonstrate that muscle associated with leg swing (i.e. iliopsoas, iliacus, rectus  
339 femoris, ...) do play an important role and therefore future studies may want to collect muscle  
340 activity data of those muscles.

341 In conclusion, we found that increasing stride frequency reduces average positive ankle power  
342 during ground contact while it more than proportionally increases average positive hip power  
343 during leg swing. Our results further build on the hypothesis that the optimal stride frequency  
344 represents a trade-off between minimizing the ground contact cost, here estimated by positive



345 ankle joint power during ground contact, and minimizing the swing cost, estimated as hip joint  
346 power during leg swing, without substantially reducing the time to produce the necessary force.  
347 Additionally, running with an increased stride frequency is often recommended as a simple  
348 strategy to reduce knee joint loading (22,38), yet our results demonstrate that, from a  
349 performance point of view, it may not be the most appropriate strategy.

### 350 **Acknowledgement**

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354 presented clearly, honestly, and without fabrication, falsification, or inappropriate data  
355 manipulation and do not constitute endorsement by ACSM.

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